

THE FUNCTIONS OF NEMATOCYSTS IN PREY CAPTURE BY EPIPELAGIC SIPHONOPHORES (COELENTERATA, HYDROZOA)¹

JENNIFER E. PURCELL²

Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543

ABSTRACT

The nematocysts of 24 siphonophore species were examined by light and scanning electron microscopy (SEM) for differences that could relate to differences in the sizes and types of prey captured. The siphonophore species in the suborder Calycophorae had 4–30 microbasic mastigophores (0.7–18.0 μl volume), and 50–2000 smaller homotrichous anisorhizas in uncoiled nematocyst batteries. The physonect siphonophore species had 4–120 stenoteles or microbasic mastigophores (1.8–40.7 μl volume), and 150–20,500 smaller homotrichous anisorhizas in coiled nematocyst batteries. The sizes of crustacean prey (primarily copepods) captured by species in both suborders increased with increasing nematocyst size and numbers. Examination by SEM of captured, but uningested prey showed that the heavily-spined threads of these nematocysts adhered to the prey surface, and primarily entangled the prey. In contrast, the tentacles of siphonophores in the suborder Cystonectae, which includes *Physalia physalis*, have only isorhizas of 1.0–18.0 μl volume with and without small spines on the threads. These nematocysts penetrate the soft-bodied prey (mostly fish larvae) of these siphonophores, but apparently do not penetrate or entangle hard-bodied prey. Thus prey capture by siphonophores differs with the sizes, numbers, and types of nematocysts present in each species. The possible functions of nematocyst batteries in tentacle spreading, and luring of large zooplankton prey are discussed.

INTRODUCTION

Siphonophore species differ in the sizes and types of prey they capture (Purcell, 1980, 1981c). This is especially intriguing because these gelatinous zooplankters appear to be passive feeders, drifting in the water with their tentacles spread (Fig. 1), and depending on prey to swim into contact with them. Dietary trends exist among the three siphonophore suborders: most calycophorans feed primarily upon small copepods; most physonects consume larger zooplankton, including copepods and other crustaceans; and cystonects consume soft-bodied prey, primarily larval fish (Purcell, 1980, 1981a, c, submitted). These dietary trends are related to behavioral and morphological characteristics of the siphonophores (Purcell, 1980). Species which consume small copepods generally swim rapidly in an arc or spiral to spread their closely-spaced tentacles, and have numerous, small gastrozooids (“stomachs”) (Fig. 1). In contrast, siphonophores that consume large zooplankton generally do not swim rapidly to spread their more widely-spaced tentacles, and have fewer, large gastrozooids.

The structures directly responsible for prey capture are the nematocysts in the tentacles. Calycophoran and physonect nematocysts are concentrated in nematocyst

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¹ Contribution no. 5495 from the Woods Hole Oceanographic Institution.

² Present address: Department of Biology, University of Victoria, Victoria, British Columbia, Canada V8W 2Y2.



FIGURE 1. *Sulculeolaria quadrivalvis* (Suborder Calycophorae) in feeding posture with tentacles spread. The tentacles appear as a string of dots, which are the nematocyst batteries. n = Nectophores (swimming bells), g = Chain of gastrozooids (stomachs). Scale = 2 cm. Photograph by J. M. King.

batteries, one battery on each of several side branches (tentilla) of the tentacles. Nematocyst batteries consist of a cnidoband with many nematocysts, several larger nematocysts along the cnidoband, an elastic ligament, and 1 or 2 terminal filaments. The battery nematocysts fire as a unit when the terminal filaments are pulled and

stretch the elastic ligament. Cystonect nematocysts are not found in these complex batteries, but may be concentrated in clumps or bands in the tentacles.

Nematocysts are classified according to the structure of the thread, which is coiled within the nematocyst capsule and everts upon discharge (reviewed in Mariscal, 1974). Historical works on siphonophore nematocysts have dealt primarily with systematic classification and the processes of nematocyst formation and discharge (Chun, 1891, 1892; Iwanzoff, 1896; Schneider, 1899, 1900; Weill, 1934; Russell, 1938, 1939; Werner, 1965). More recently, siphonophore nematocysts have been used to elucidate the process of nematocyst development (Carré, 1972, 1974a, b, c; Carré and Carré, 1973; Skaer, 1973).

Different functions have been ascribed to some of the various types of coelenterate nematocysts based on the structure of the thread, or on correlation of certain nematocyst types with specific functions. For example, an anacrophore is called a glutinant because the thread is closed at the tip while other types are presumed to be penetrants because the thread is open at the tip (Mariscal, 1974); holotrichous isorhizas in the acroraghi and catch tentacles of sea anemones presumably penetrate the victims of inter- and intraspecific agonistic interactions (Francis, 1973; Purcell, 1977). The discharge of nematocysts on prey organisms has been investigated only in *Hydra*; Toppe (1909), Ewer (1947), and Tardent and Holstein (1982) found that prey were penetrated by stenoteles and were entangled by desmonemes. Observations in Schwartz *et al.* (1983) suggest that a particular cladoceran species, which was not captured often by *Hydra* spp., might not be penetrated by the nematocysts of *Hydra*, might not stimulate the nematocysts to fire, or might be immune to the toxins. The present paper summarizes the characteristics of the nematocyst batteries and nematocysts of the three siphonophore suborders, and examines differences in the nematocysts that may mediate the differential prey capture seen in several siphonophore species.

MATERIALS AND METHODS

Prey size analysis

Siphonophores were collected in jars by SCUBA divers at 5–25 m depth primarily in the Gulf of California, the Gulf Stream, and the Sargasso Sea. Details of the methods, and of the locations and dates for collection of most siphonophores used in analysis of prey size are given in Purcell (1981c). Additional dietary data came from specimens collected during August, 1981 in the North Atlantic along the 25°N parallel, and during February and May, 1982 in the Sargasso Sea (approximately 30°77–78°W and 34°N 73°W, respectively), and in the Gulf Stream (approximately 32°N 78°W to 36°N 72°W and 33°N 77°W to 36°N 73°W). The cephalothorax length of copepods was measured using an optical micrometer at 25–400× magnification.

Microscopy

Siphonophores used for scanning electron microscopy (SEM) were collected primarily in the North Atlantic during August, 1981, as above. When the siphonophores had assumed a feeding posture with tentacles spread in 4 l clear plastic containers aboard ship, active copepods, chaetognaths, or fish larvae from plankton tows were released individually near the tentacles by pipette. The captured prey were retrieved with forceps after the prey swam into contact with the siphonophore tentacles, but before they could be ingested. Specimens were placed in 2% gluteraldehyde in sea

water for 1 h, postfixed in 1% OsO₄ in sea water for 1 h, transferred at 10 min intervals into 30%, 50%, and 70% ethanol and stored at 4°C. Ethanol dehydration was followed by critical-point drying with CO₂ or Freon in a Tousimas sam-dry-780 or a Bowmar SPC-900 critical-point drying chamber. Specimens were mounted on stubs, rotary-coated with gold in a Denton DSM-5 or an International Scientific Instruments (ISI) PS-2 vacuum evaporator, and examined in a JEOLCO V3 or an ISI Alpha-9 scanning electron microscope in order to examine the effect of nematocysts on prey. Small pieces of Nitex screen were swept through extended tentacles and treated as above, in order to examine the thread structure of discharged nematocysts. One or 2 copepods, and 1 screen were examined for each siphonophore species.

Siphonophores used for light microscopy first were relaxed in MgCl₂ in sea water until the tentacles no longer contracted when touched, and then preserved in 5% formalin. The length, width, and depth of nematocyst batteries were measured at 40–400× magnification on a compound microscope with an optical micrometer. The maximum length and width of undischarged nematocysts from disrupted batteries were measured at 400–1000×. The numbers of anisorhizas (haplonemes) were approximated from the surface area (length × width) of the cnidoband divided by the maximum cross-sectional area of the anisorhizas; the depth of the cnidoband corresponds to their length. The large microbasic mastigophores and stenoteles (heteronemes) were counted, and their volumes were estimated according to the formula for the volume of an ellipsoid, $4ab^2/3$, where a = length/2, and b = diameter/2. The dimensions of at least 5 nematocysts of each type were measured for each specimen, and 2–6 specimens were examined in each species. The measurements are from one specimen, or are maximum and minimum values where substantial differences existed among several specimens within a species.

Terminology

Nematocyst classification and terminology used herein is as presented by Mariscal (1974) based on the structure of the nematocyst thread (Fig. 2). Simply, haplonemes are nematocysts without a well-defined shaft at the base of the thread; isorhizas have threads of equal diameter throughout, while the base of the thread of an anisorhiza is slightly dilated; holotrichous indicates that spines occur along the length of the thread, and atrichous threads have no spines. Heteronemes have a well-defined shaft; microbasic mastigophores have a short shaft of equal diameter throughout; stenoteles have a short shaft of unequal diameter, with 3 well-developed spines. Desmonemes, acrophores, and anacrophores have threads with closed tips and no spines.

RESULTS

Measurements and photographs of nematocyst batteries and nematocysts are presented for the 3 siphonophore suborders: Calycophorae (Table I, Fig. 3), Physonectae (Table II, Fig. 4), and Cystonectae (Table III, Fig. 5). Each table and figure has been organized by siphonophore family, and arranged in order of increasing nematocyst and nematocyst battery sizes, as far as was possible. Differences in corresponding nematocyst dimensions in the tables and figures may be due to effects of preservation, and to a 20% reduction in length and diameter in capsules of discharged nematocysts (Tardent and Holstein, 1982). The batteries and nematocysts were similar enough among species of each family that only representative illustrations are given for each family in Figures 3, 4, and 5.

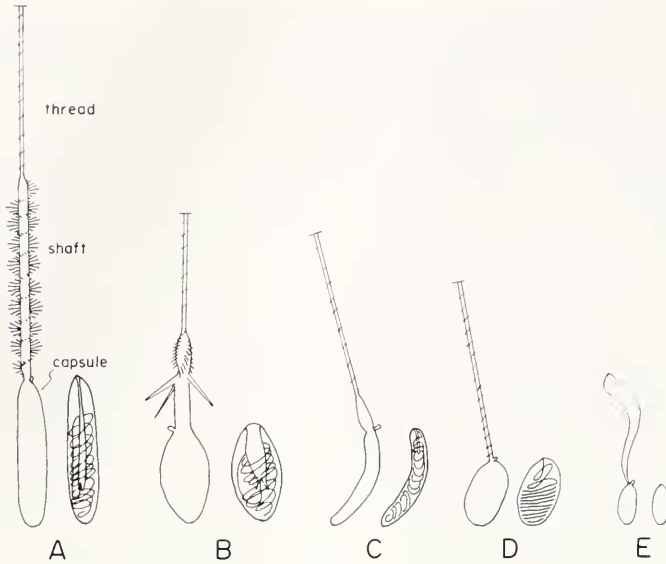


FIGURE 2. Discharged and undischarged nematocysts from siphonophore tentacles. A. Microbasic mastigophores (heteronemes). B. *Stenoteles* (heteronemes). C. *Holotrichous anisorhizas* (haplonemes). D. *Holotrichous isorhizas* (haplonemes). E. *Anacrophore* (rhopalonemes). After Iwanzoff (1896).

Suborders *Calycophorae* and *Physonectae*

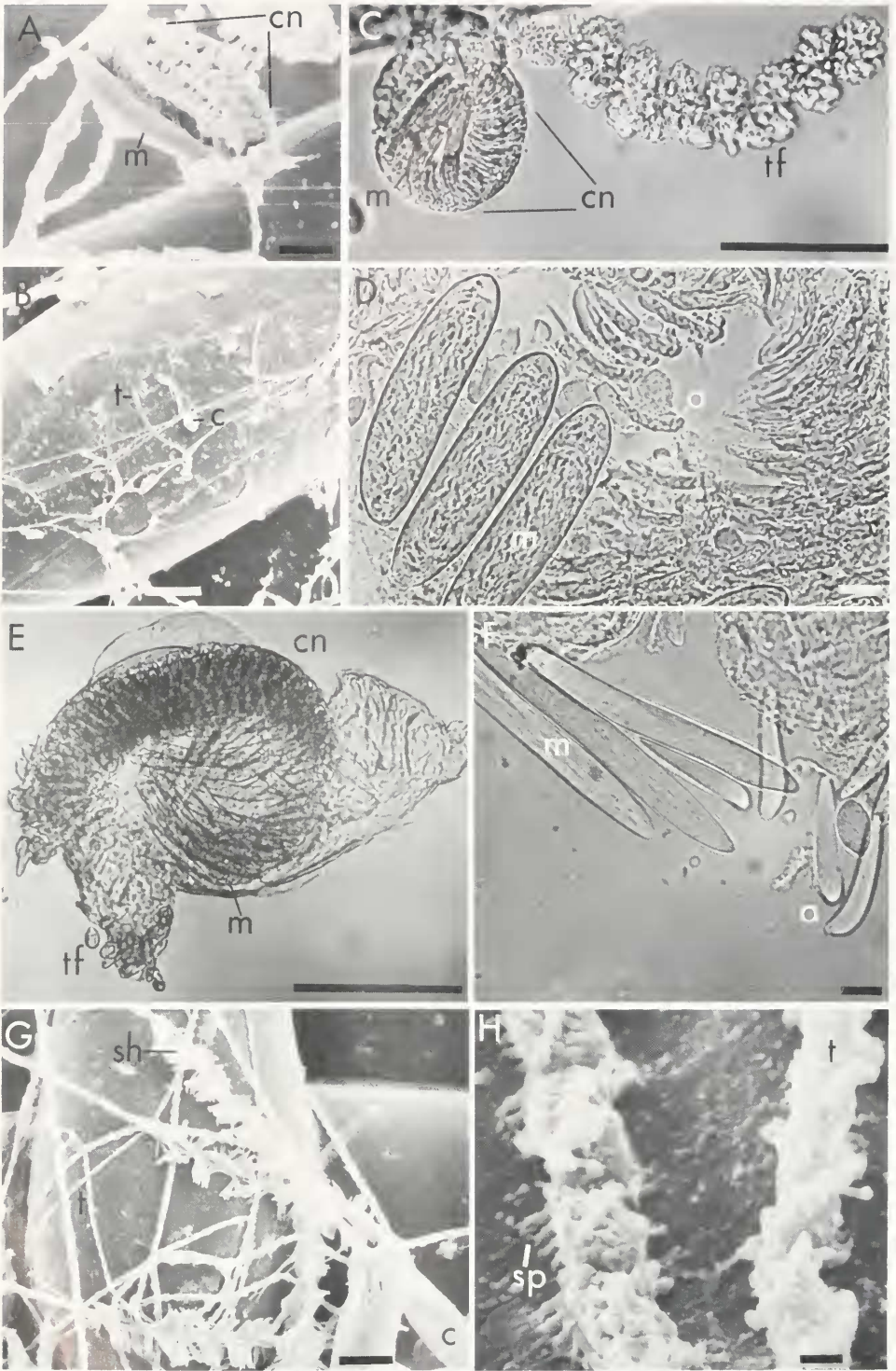
Each of the species examined in these suborders had nematocyst batteries that contained numerous haplonemes of one type in the cnidoband and several larger heteronemes of one type, and 1 or 2 types of small nematocysts in the terminal filaments. The nematocyst battery structure was consistent within each suborder, but sizes of nematocysts differed among species (Tables I and II). The ranges of nematocyst sizes within species in Tables I and II result from the fact that small specimens within a species had fewer and somewhat smaller heteronemes than large specimens. This fact may explain differences in measurements made by other authors, as follow. An increase in the cnidoband length with siphonophore size was also noticeable in *Stephanophyes superba*, *Athorybia rosacea*, *Forskalia edwardsi*, and *Agalma* spp., where specimens spanning a large size range were available. Large specimens were used in calculations of the numbers of anisorhizas (haplonemes, Tables I and II) and volumes of the heteronemes (Table IV).

The nematocyst batteries of the calycophoran species within the families Sphaeronectidae, Diphyidae, and Abylidae were alike, having a long, straight cnidoband (Fig. 4A, I, L); those of the families Hippopodiidae and Prayidae were more rounded (Fig. 4C, E). The holotrichous anisorhizas (haplonemes) (Fig. 3D, F, N) of the uncoiled cnidoband of calycophorans were classified by Weill (1934) in *Eudoxoides* (= *Diphyes*) *spiralis* (Bigelow, 1911) (22×6 – $32 \times 7 \mu\text{m}$), *Hippopodius hippopus* (= *neapolitanus*) ($30 \times 5 \mu\text{m}$), *Rosacea* (= *Praya*) *cymbiformis* [$60 \times 6.5 \mu\text{m}$, data from Iwanzoff (1896), where identification of the specimen was uncertain; those measurements and those for the heteronemes (below) differ greatly from those on *R. cymbiformis* in Table I], and *Abylopsis tetragona* ($62 \times 10 \mu\text{m}$). Russell (1939) described the haplonemes of *Muggiaea atlantica* as atrichous anisorhizas (13 – 18×3 – $4 \mu\text{m}$). The elongate heteronemes were microbasic mastigophores (Fig. 3A, C, D, E, F, G, I), as classified by Weill (1934) for *E. spiralis* (62×9 – $85 \times 11 \mu\text{m}$), *H. hippopus* (90×17 –

TABLE I

Battery nematocysts of siphonophores in the suborder Calycophorae

	Battery dimensions (μm)	Cnidoband			Terminal filament nematocysts (μm)	
		Heteronemes		Haplonemes		
		(μm)	(No.)	(μm)		(No.)
Family Sphaeronectidae						
<i>Sphaeronectes gracilis</i> (Claus, 1873)	48 × 26 × 18	36.0 × 7.0	4	12.0 × 2.0 7.0 × 5.0	50	4.0 × 3.0 3.0 × 1.5
Family Hippododiidae						
<i>Hippododus hippopus</i> (Forsk., 1776)	96 × 96 × 46	78.0–84.0 × 17.0	7–10	26.0 × 5.5	200	6.0 × 6.0
Family Prayidae						
<i>Rosacea cymbiformis</i> (Chiaje, 1822)	255 × 120 × 50	67.0 × 8.0	25–30	32.0 × 6.0 11.0 × 7.0	400	9.6 × 4.4 8.0 × 8.0
<i>Stephanophyes superba</i> (Chun, 1888)	1500 × 60 × 84	111.0 × 13.0	32–50	45.0 × 9.0 23.0 × 13.0	2000	27.0 × 9.0 18.0 × 10.0
Family Diphyidae						
<i>Muggiaca atlantica</i> (Cunningham, 1892)	120 × 52 × 30	36.0 × 6.0	6	15.0 × 4.0 9.0 × 6.0	300	6.0 × 4.0 6.0 × 2.0
<i>Chelophyes appendiculata</i> (Eschscholtz, 1829)	150 × 52 × 36	66.0 × 6.0	6	15.5 × 4.0 12.0 × 7.0	450	10.0 × 6.0 9.0 × 3.0
<i>Sulculeolaria quadrivalvis</i> (Blainville, 1934)	114 × 66 × 30	47.5 × 7.5	8	20.0 × 5.0 12.5 × 9.5	200	7.5 × 2.5 7.5 × 7.5
<i>S. monoica</i> (Chun, 1888)	168 × 66 × 30	60.0 × 10.0	8	22.5 × 5.5 12.5 × 10.0	—	12.5 × 5.0
<i>Diphyes dispar</i> (Chamisso and Eysenhardt, 1821)	270 × 78 × 42	97.5 × 11.0	12	15.0 × 7.5 20.0 × 12.0	250	15.0 × 9.0
Family Abylidae						
<i>Basfia bassensis</i> (Quoy and Gaimard, 1833)	315 × 100 × 70	75.5 × 14.0	8	36.0 × 8.5 14.0 × 9.0	400	11.0 × 8.0 12.0 × 4.0
<i>Abylopsis tetragona</i> (Quoy and Gaimard, 1827)	891 × 198 × 70	145.0–155.0 × 15.0	20–21	52.5 × 10.0 25.0 × 12.5	800	23.0 × 3.0 15.0 × 5.0
<i>Abyla trigona</i> (Quoy and Gaimard, 1827)	396 × 248 × 120	153.0 × 15.0	11–13	54.0 × 12.5 23.0 × 12	400	15.0 × 5.0



The following abbreviations are used in Figures 3–5: a = anisorhiza, c = nematocyst capsule, cn = cnidoband, cl = elastic ligament, i = isorhiza, m = microbasal mastigophore, t = nematocyst thread, tf = terminal filament, s = stenotele, sh = nematocyst shaft, and sp = spines on nematocyst thread.

FIGURE 3. Suborder Calycophorae. A. Nematocyst battery of *Sphaeronectes gracilis* (Fam. Sphaeronectidae), 1000 \times , scale = 10 μ m. B. Nematocysts (anacrophores) from the terminal filaments of *S.*

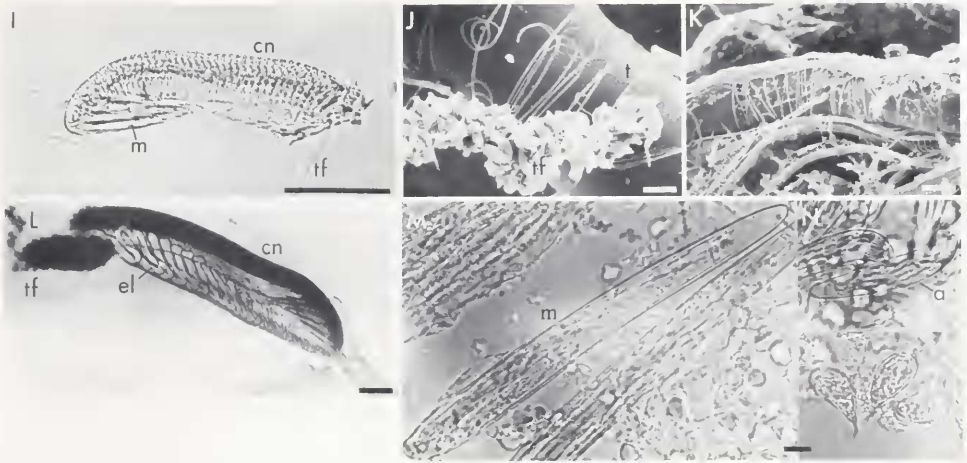


FIGURE 3 (con't). I. Nematocyst battery of *Diphyes dispar* (Fam. Diphyidae), 160 \times , scale = 100 μ m. J. Terminal filament of *Sulculeolaria quadrivalvis* (Fam. Diphyidae), 1000 \times , scale = 10 μ m. K. Copepod antenna wrapped by the nematocyst threads of *S. quadrivalvis*, 400 \times , scale = 25 μ m. L. Nematocyst battery of *Abylopsis tetragona* (Fam. Abylidae), 50 \times , scale = 100 μ m. M, N, O. Nematocysts of *Abyla trigona*: M. Large heteronemes, N. Haplonemes (anisorhizas) from the cnidoband, O. Haplonemes (isorhizas) from the battery tip. 400 \times scale = 10 μ m.

95 \times 18 μ m), *R. cymbiformis* (250 \times 16 μ m), and *A. tetragona* (195 \times 17 μ m); and by Russell (1938) for *M. atlantica* (36–43 \times 6–7.5 μ m), with prominent spines on the shaft (Fig. 3G) and smaller spines along the remainder of the thread (Fig. 3H). Heteronemes of *Stephanophyes superba* and *Diphyes dispar* (= *Dormasia picta*) were measured at 120 μ m and 100 μ m in length by Chun (1891) and (1892), respectively. At the free end of the batteries were several smaller rounded nematocysts (3E, I, L, O), probably holotrichous isorhizas (haplonemes, as pictured in Iwanzoff, 1896), with long cnidocils, the ciliary sensory receptors which trigger nematocyst discharge (e.g., Carré and Carré, 1980). The single terminal filament on each battery contained nematocysts with club-shaped threads; anacrophores (Fig. 3B), as identified by Weill (1934) in *E. spiralis* (5–6 \times 2 μ m), *H. hippopus* (12 μ m), *R. cymbiformis* (22 \times 8 μ m), and *A. tetragona* (22 \times 8 μ m), and by Russell (1938) in *M. atlantica* (5–6 \times 2 μ m), and/or desmonemes as identified by Weill (1934) in *E. spiralis* (7–10 \times 4–6 μ m), *H. hippopus* (7 \times 7.5 μ m), and *A. tetragona* (30 \times 13 μ m), and by Russell (1938) in *M. atlantica* (7–10 \times 4–6 μ m). Some measurements of nematocysts in the batteries of other calycophoran species exist: (Family Diphyidae) *Dimophyes arctica* (Chun, 1897), heteronemes 280 μ m, *Lensia conoidea* (Kefferstein and Ehlers, 1860), heteronemes \sim 53 \times 7 μ m; *Sulculeolaria biloba* (Sars, 1846), heteronemes = 56–58 \times 7–8 μ m, haplonemes = 19–24 \times 3–5 μ m and 9–11 \times 7–8 μ m (in Totton, 1965); (Family Abylidae) *Enneagonium hyalinum* (Quoy and Gaimard, 1827), heteronemes = 80 μ m long, haplonemes = 40 μ m long (in Chun, 1892). The terminal filaments of *Sulculeolaria* spp., especially *S. quadrivalvis*, were very adhesive, and had haplonemes with holotrichous threads (Fig. 3J).

gracilis. 1000 \times , scale = 10 μ m. C. Nematocyst battery of *Hippopodius hippopus* (Fam. Hippopodiidae) 160 \times , scale = 10 μ m. D. Nematocysts of *H. Hippopus*, 400 \times , scale = 10 μ m. E. Nematocyst battery of *Rosacea cymbiformis* (Fam. Prayidae), 160 \times , scale = 100 μ m. F. Nematocysts of *R. cymbiformis*, 400 \times , scale = 10 μ m. G. Discharged nematocysts (microbasic mastigophores) of *R. cymbiformis*, 1000 \times , scale = 10 μ m. H. Nematocyst threads of *R. cymbiformis* adhering to the surface of a chaetognath, 8000 \times , scale = 1 μ m.

TABLE II

Battery nematocysts of siphonophores in the suborder Physonectae

	Battery dimensions (μm)	Cnidoband				Terminal filament nematocysts (μm)
		Heteronemes		Haplonemes		
		(μm)	(No.)	(μm)	(No.)	
Family Athorybiidae <i>Athorybia rosacea</i> (Forsk., 1775)	102 × 60 × 60	65.0 × 22.5	4-50	32.5 × 7.5	800	7.0 × 2.5 5.0 × 5.0
Family Forskaliidae <i>Forskalia edwardsi</i> (Kölliker, 1853)	420 × 180 × 180	38.0 × 22.5	20-30	30.0 × 5.5	3000	13.0 × 5.0
Family Agalmidae <i>Cordagalma cordiformis</i> (Totton, 1932)	50 × 32.5 × 32.5	22.5 × 12.5	4-7	22.5 × 6.0 6.0 × 6.0	150	3.0 × 4.5
<i>Nanomia bijuga</i> (Chiaje, 1841)	445 × 248 × 240	32.0 × 16.0	15-35	22.5 × 5.5	4500	11.0 × 4.5
<i>Nanomia cara</i> (A. Agassiz, 1865)	1400 × 680 × 680	62.5 × 22.5	70-80	72.5 × 12.5	14,000	17.5 × 10.0 12.5 × 10.0
<i>Agalma elegans</i> (Sars, 1846)	396 × 120 × 120	130.0 × 20.0-180.0 × 28.0	11-30	35.0 × 5.0	17,000	5.0 × 5.0-7.5 × 7.5
<i>Agalma okeni</i> (Eschscholtz, 1825)	1164 × 680 × 680	112.5 × 20.0-135.0 × 24.0	30-120	47.5 × 6.0	20,500	7.0-7.0
Family Physophoridae <i>Physophora hydrostatica</i> (Forsk., 1775)	1260 × 390 × 390	109.0 × 29.0	—	32.5 × 6.2	—	—

The nematocyst batteries of physonect siphonophores had a spirally coiled cnidoband (Fig. 4A, D, K), with the exceptions of *Cordagalma cordiformis* in which it is short and uncoiled (Fig. 4G, H), and *Physophora hydrostatica* in which it is loosely coiled (Fig. 4Q). The holotrichous anisorhizas (Fig. 4C, G, L, M) of the cnidoband of physonects were classified by Weill (1934) in *Forskalia* sp. ($37\ \mu\text{m}$ long), *Physophora hydrostatica* [$30\text{--}30.5 \times 7\text{--}7.5\ \mu\text{m}$ (Iwanzoff, 1896)], *Agalma clausi* (Bedot, 1888) ($60\ \mu\text{m}$ long) and *Agalma elegans* (= *sarsi*)/*Agalma* (= *Agalmopsis*) *elegans* ($22 \times 12\ \mu\text{m}$), and by Russell (1939) in *A. elegans* (up to $75 \times 6\text{--}7\ \mu\text{m}$), and by Carré (1968) in *Cordagalma cordiformis* ($16 \times 2\ \mu\text{m}$). The large, ovoid heteronemes were stenoteles in most species examined: *Athorybia rosacea* (Fig. 4B, C, as in Schneider, 1900), *Forskalia* spp. [Fig. 4E, as in Weill, 1934 ($55 \times 25\ \mu\text{m}$)], *Cordagalma cordiformis* [Fig. 4G, as in Carré, 1968 ($17.5 \times 8.5\ \mu\text{m}$)], *Namomia bijuga* (Fig. 4L, N, probably also *N. cara*), and *Physophora hydrostatica* [Fig. 4Q, R, S, as in Schneider (1900) although Iwanzoff (1896) shows microbasic mastigophores $\sim 100\text{--}150\ \mu\text{m}$ long]; but were microbasic mastigophores in *Agalma elegans* [Fig. 4O, P, as in Iwanzoff, 1896 ($90 \times 30\ \mu\text{m}$); Weill, 1934; and Russell, 1939 ($185\text{--}205 \times 25\text{--}28\ \mu\text{m}$)], *A. clausi* [in Weill, 1934 ($220\ \mu\text{m}$ long)], and probably also in *A. okeni*. *Cordagalma cordiformis* also had several rounded isorhizas at the battery tip (as in Carré, 1968). The 1 or 2 terminal filaments per battery had 1 or 2 nematocyst types, classified in Weill (1934) as acrophores and desmonemes in *Forskalia* sp. ($15 \times 7.5\ \mu\text{m}$), *A. clausi* ($20\ \mu\text{m}$ long, and $12.5\text{--}12.5\ \mu\text{m}$), and *A. elegans* ($21 \times 15\ \mu\text{m}$ and $10 \times 10\ \mu\text{m}$), and in Russell (1938) as anacrophores and desmonemes in *A. elegans* ($7 \times 2\text{--}20 \times 5\ \mu\text{m}$ and $6\text{--}7 \times 6\ \mu\text{m}$). *Halistemma rubrum* (Vogt, 1852) (Family Agalmidae) is reported to have nematocysts $60\text{--}65 \times 7\ \mu\text{m}$ (haplonemes) and $65\text{--}70 \times 20\ \mu\text{m}$ (heteronemes) in the cnidoband (Totton, 1965), although Iwanzoff (1896) comments on the enormous size of the nematocysts ($1120 \times 120\ \mu\text{m}$). *Apolemia uvaria* (Lesueur, 1811) (Family Apolemiidae) is an unusual physonect species in that it lacks nematocyst batteries. The nematocysts in the tentacles (birhophaloides, 24×15 and $15 \times 9\ \mu\text{m}$) have a thread with two dilations near the base, and are unique to *A. uvaria* (as in Carré and Carré, 1973). The diet is also unusual in having a large proportion of gelatinous zooplankton (Purcell, 1981c).

The species of calycophoran and physonect siphonophores for which dietary data are available are listed in Table IV, arranged in order of increasing mean size of copepods found in the gastrozooids. Copepods comprised 80–100% of the prey organisms in the calycophorans examined, but only 14–80% in the physonectids, which generally contained a variety of larger zooplankton [hyperiid amphipods, decapod larvae, and “shrimp” (including euphausiids)] (Purcell, 1980, 1981c). Thus, mean prey sizes based only on copepods underestimate the actual sizes of prey consumed by physonects. Even so, prey size was positively correlated with nematocyst size, expressed as the volume of the large heteronemes ($P < 0.001$, Kendall Rank Correlation, Sokal and Rohlf, 1969). Species with large heteronemes also tended to have larger haplonemes in the cnidoband (Tables I and II; $P < 0.05$, Kendall Rank Correlation). The total number of nematocysts in a battery also was significantly correlated with prey size ($P < 0.01$). Thus, as numbers and sizes of nematocysts in batteries increased, so did the size of prey captured by the various species. This trend would be stronger if prey other than copepods were considered in the analysis. The numbers of nematocyst batteries per tentacle, the numbers of tentacles per siphonophore, and the total numbers of batteries per siphonophore display a general tendency for species that capture large prey to have fewer tentacles, and fewer (but larger) batteries per tentacle (Table IV). These values span the range found in the available specimens, but should not be understood to represent the limits for any species; colonies of *Rosacea cymbiformis*

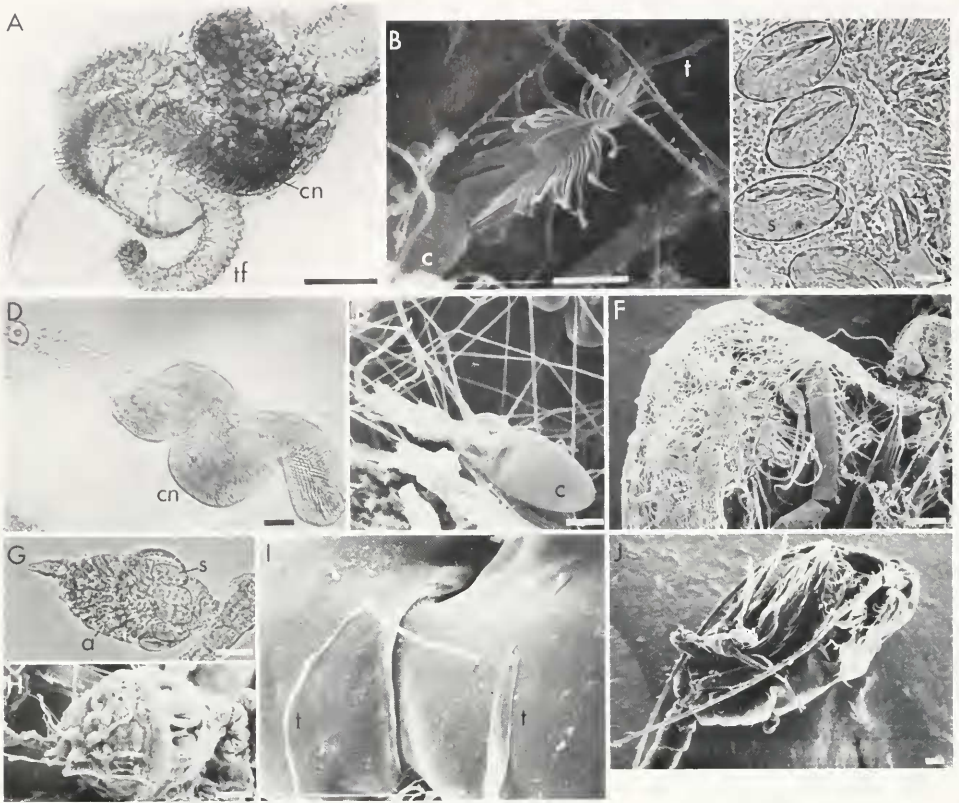


FIGURE 4. Suborder Physonectae. A. Nematocyst battery of *Athorybia rosacea* (Fam. Athorybiidae), 100 \times , scale = 100 μ m. B. Nematocyst shaft of a stenotele from *A. rosacea*, 2000 \times , scale = 10 μ m. C. Nematocysts of *A. rosacea*, 400 \times , scale = 10 μ m. D. Nematocyst battery of *Forskalia edwardsi* (Fam. Forskaliidae), 40 \times , scale = 100 μ m. E. Nematocyst (stenotele) of *F. edwardsi*, 1000 \times , scale = 10 μ m. F. Copepod captured by *F. edwardsi*, 100 \times , scale = 100 μ m. G. Nematocyst battery of *Cordagalma cordiformis* (Fam. Agalmidae), 200 \times , scale = 25 μ m. H. Nematocyst battery of *C. cordiformis*, 1000 \times , scale = 10 μ m. I. Nematocyst threads of *C. cordiformis* adhering to a copepod, 1000 \times , scale = 10 μ m. J. Uncaptured copepod, 50 \times , scale = 100 μ m.

and *Stephanophyes superba*, in particular, reach much greater lengths, and therefore have many more tentacles.

The effect of calycophoran and physonect nematocysts on prey was dramatic—the nematocyst threads wrapped and entangled copepod prey (Fig. 3K; 4F, M). Nematocyst threads with and without spines adhered to the surfaces of copepods, chaetognaths, and Nitex fibers (Fig. 3B, G, H, J, K; 4I, M). The spines along the length of the threads were affixed to the prey surface wherever they were in contact. The flattened threads of *Cordagalma cordiformis* nematocysts were unlike the tubular threads of other species; the tips of these unspined threads clearly adhered to crustaceans (Fig. 4I). Penetration of the exoskeleton by the nematocyst threads was not obvious in any of the copepods prepared for SEM. Threads may have entered joints in the exoskeleton in a few cases, such as when the stenoteles of *Nanomia bijuga* oriented along the cephalothorax/abdominal joint of a copepod (Fig. 4N). Nematocyst threads penetrated, as well as adhered to soft-bodied prey.

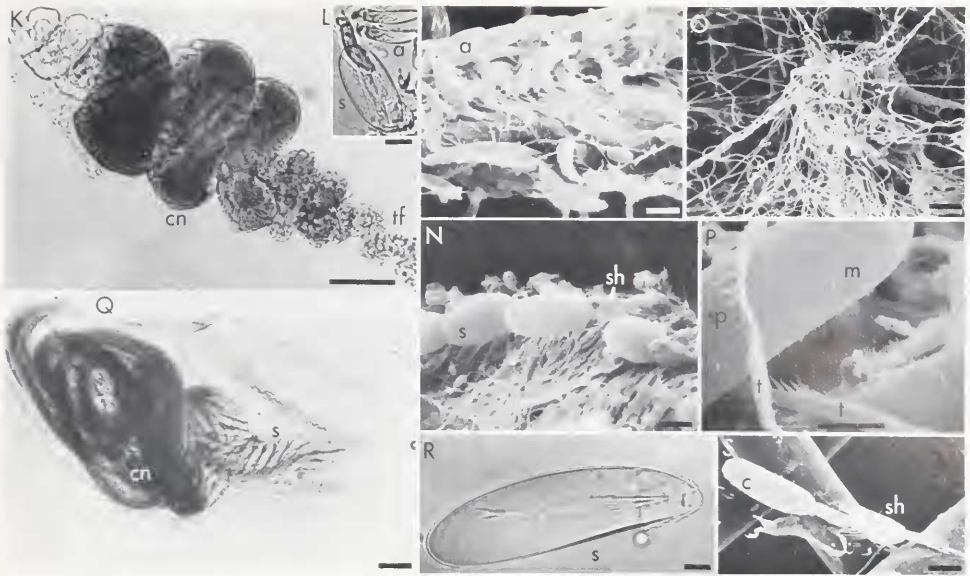


FIGURE 4. (con't). K. Nematocyst battery of *Nanomia bijuga* (Fam. Agalmidae), 100 \times , scale = 100 μ m. L. Nematocysts of *N. bijuga*, 400 \times , scale = 10 μ m. M. and N. Nematocysts of *N. bijuga* discharged on a copepod antenna, and along the cephalothorax/abdominal joint, 1000 \times , scales = 10 μ m. O. Discharged nematocyst battery of *Agalma okeni* (Fam. Agalmidae), 100 \times , scale = 100 μ m. P. Nematocyst threads of *A. okeni*, 2000 \times , scale = 5 μ m. Q. Nematocyst battery of *Physophora hydrostatica* (Fam. Physophoridae), 50 \times , scale = 100 μ m. R. Nematocyst of *P. hydrostatica*, 400 \times , scale = 10 μ m. S. Discharged stenotele of *P. hydrostatica*, 400 \times , scale = 25 μ m.

Suborder Cystonectae

The tentacles of cystonect siphonophores lack complex nematocyst batteries (Fig. 5A, E), but nematocysts occur in bands in *Physalia physalis* (Fig. 5A) and in clusters in *Rhizophysa filiformis* (Fig. 5F). All nematocysts in cystonect tentacles are haplonemes (isorhizas) (Table III, Fig. 5B, G, H). Homotrichous threads with minute spines were found in *Physalia physalis* (Fig. 5C, as in Mackie, 1960; and Cormier

TABLE III

Tentacle nematocysts of siphonophores in the suborder Cystonectae

	Haplonemes (μ m)
Family Physalidae	
<i>Physalia physalis</i>	27.5 \times 27.5
(L) 1758	12.5 \times 12.5
Family Rhizophysidae	
<i>Bathypphysa sibogae</i>	17.0 \times 17.0
(Lens and van Riemsdijk, 1908)	10.0 \times 10.0
<i>Rhizophysa filiformis</i>	32.5 \times 32.5
(Forskal, 1775)	12.5 \times 12.5
<i>Rhizophysa eysenhardti</i>	
(Gegenbaur, 1859)	20.0 \times 20.0

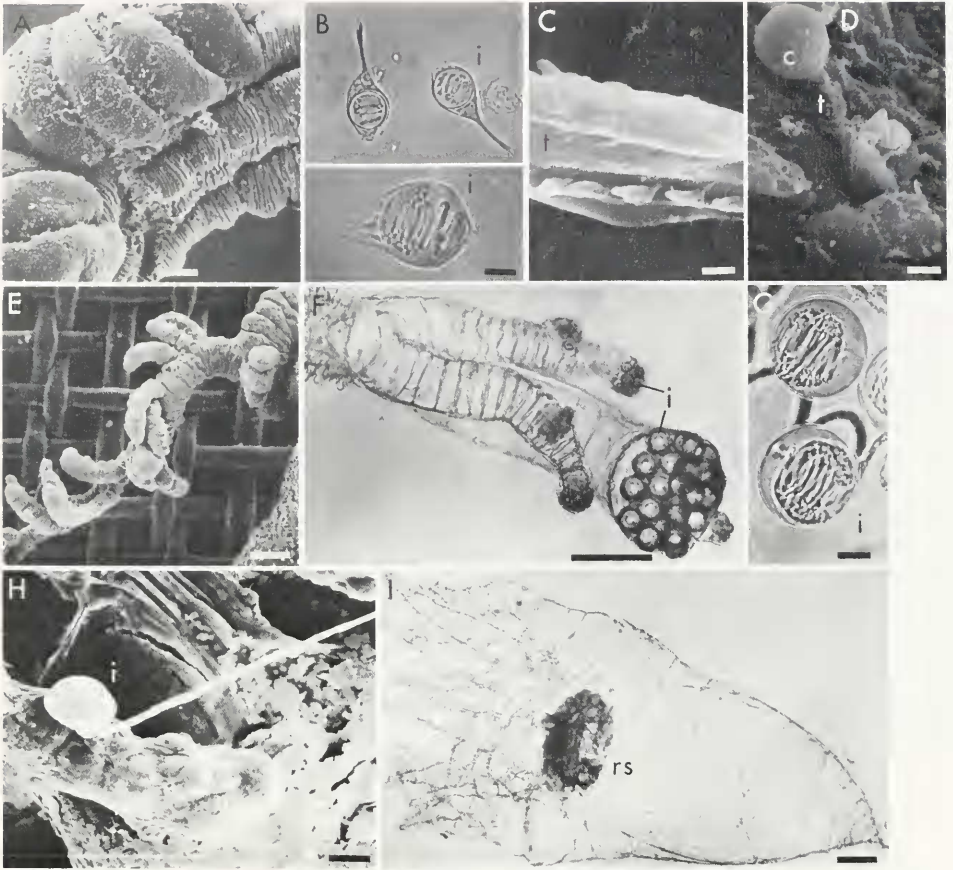


FIGURE 5. Suborder Cystonectae. A. Portion of unbranched tentacle of *Physalia physalis* (Fam. Physaliidae), 50 \times , scale = 200 μ m. B. Nematocysts of *P. physalis* in cells with fibrillar attachments to the tentacles, 400 \times , scale = 10 μ m. C. Nematocyst thread of *P. physalis*, 8000 \times , scale = 1 μ m. D. Nematocyst of *Rhizophysa eysenhardti* (Fam. Rhizophysidae) penetrating under the scales of a fish larva, 1000 \times , scale = 10 μ m. E. Branched tentacle of *Rhizophysa eysenhardti*, 100 \times , scale = 100 μ m. F. Tentacle tip of *R. filiformis*, 100 \times , scale = 100 μ m. G. Nematocysts of *R. filiformis*, 400 \times , scale = 10 μ m. H. Discharged nematocyst of *R. eysenhardti*, 1000 \times , scale = 10 μ m. I. Appendage with a red spot (rs) from the tentacles of *R. filiformis*, 25 \times , scale = 200 μ m.

and Hessinger, 1980) and *R. filiformis*, and apparently atrichous threads in *R. filiformis* and *R. eysenhardti* (Fig. 5H). The spines on the nematocyst threads of *P. physalis* are too small to be discerned with certainty by light microscopy; therefore the nematocysts were thought to be atrichous isorhizas [Weill, 1934, *Physalia arethusa* (= *physalis*), 15–42 μ m diameter; Totton, 1960; also measured by Lane and Dodge, 1958 (26.8 \times 26.8 μ m and 11.3 \times 11.3 μ m)].

The nematocysts of cystonects are much less diverse than those of calycophorans and physonects, and lack the conspicuous spination on the threads. The nematocysts are similar in size among cystonect species (Table III), and there is little diversity apparent in diet. *Physalia physalis* consumes fish larvae, small cephalopods, large chaetognaths, and leptocephalus larvae of eels (Purcell, submitted), as well as some larger fish to 10 cm in length (e.g., Wilson, 1947); the other species consume fish larvae (Purcell, 1981a, c). Those data show that cystonect siphonophores consume

TABLE IV

Calycophoran (C) and physonect (P) siphonophores listed in order of increasing prey size (copepods only)

Species	Sub-order	Mean prey size (mm)	Large nematocyst volume (μ l)*	Nematocysts per battery (no.)*	Batteries per tentacle (no.)	Tentacles (no.)	Number of batteries
<i>Muggiaca atlantica</i>	C	0.36	0.68	306	20	20-30	400-600
<i>Sphaeronectes gracilis</i>	C	0.36	0.92	54	25-30	20-60	500-1800
<i>Chelophyes appendiculata</i>	C	0.42	1.24	456	25-30	10-20	250-600
<i>Cordagalma cordiformis</i>	P	0.45	1.84	157	60-70	20-30	1200-2100
<i>Sulculeolaria quadrivalvis</i>	C	0.57	1.40	208	80-90	85-520	6800-46,800
<i>Bassia bassensis</i>	C	0.79	7.74	408	5-10	5-15	25-150
<i>Athorybia rosacea</i>	P	0.84	17.22	850	120	1-10	120-1200
<i>Hippopodius hippopus</i>	C	0.86	5.32	210	30-100	10-20	300-2000
<i>Rosacea cymbiformis</i>	C	0.98	2.25	430	80-90	10-100	800-9000
<i>Diphyes dispar</i>	C	0.99	6.46	262	40-50	90-180	3600-9000
<i>Abyla trigona</i>	C	1.10	18.02	413	10-20	10-20	100-400
<i>Forskalia edwardsi</i>	P	1.17	9.94	3030	10-20	10-320	100-6400
<i>Nanomia bijuga</i>	P	1.18	4.29	4535	15-20	15-20	225-400
<i>Agalma elegans</i>	P	1.33	27.21-73.85	17,030	12-50	5-30	60-150
<i>Stephanophyes superba</i>	C	1.52	9.82	2050	30-40	10-30	300-1200
<i>Agalma okeni</i>	P	1.97	40.69	20,620	15-35	2-9	30-315

* Calculated from values in Table I and II.

only prey lacking hard exoskeletons. Their nematocysts clearly penetrate soft-bodied prey (Fig. 5D). No discharged nematocysts penetrated or adhered to a shrimp (*Leander* sp.) that was thrust repeatedly into the tentacles of *P. physalis*. That result could be due to failure of the nematocysts to discharge or failure to affect the prey.

DISCUSSION

The large majority of the nematocysts in the battery complex of calycophorans and physonectes appear to adhere to and entangle crustaceans, their principle prey. The threads of nematocysts in the terminal filaments (anacrophores and desmonemes) have closed, rounded ends. Anisorhizas, by far the most numerous nematocysts of the cnidobands, had spines along the length of the threads which adhered to all surfaces. The long, spined shaft of microbasic mastigophores also adhered to surfaces. To date, only stenoteles in *Hydra* have been shown to penetrate crustacean exoskeleton (Toppe, 1909; Ewer, 1947; Tardent and Holstein, 1982). The stenoteles of *Hydra* are forcefully ejected from the tentacle and penetrate crustacean exoskeleton presumably by the impact of the three stylets, which form a "pointed arrowhead" (Tardent and Holstein, 1982). Mariscal (1974) cited his unpublished results that showed penetration of prey by Anthozoan microbasic p-mastigophores and basitrichous isorhizas, but did not specify the prey used. Most siphonophore nematocysts do not appear to penetrate crustacean exoskeleton. Only physonect siphonophores have penetrating stenoteles, but adhering anisorhizas outnumbered stenoteles in the cnidobands of physonectes by 20-40:1 (*C. cordiformis*) to ~200:1 (*Nanomia* spp.).

These results suggest that most nematocysts of calycophoran and physonect siphonophores function to entangle crustacean prey. The nematocyst threads clearly adhere to surfaces, however the mechanism of adhesion is unknown. Anthozoan nematocysts adhere to glass slides and to cleaned gastropod shells (e.g., Sandberg *et al.*, 1971; Mariscal, 1972). Similarly, tentaculate ctenophores rely only upon a glue

produced by colloblasts on the tentacles to adhere to, and capture, the same crustacean zooplankton prey (Franc, 1978).

The fact that the threads of most of these siphonophore nematocysts appear not to penetrate the prey raises questions about their toxicity. The toxins of siphonophore nematocysts have been examined only for *Physalia* (Cystonectae), and it has not been possible to isolate single types of nematocysts (e.g., Lane and Dodge, 1958; Burnett and Calton, 1977). Therefore, it is unknown if the nematocyst types of other siphonophores contain toxin. It is also unknown if nematocyst toxins are a liquid in the capsule which is expelled through the thread upon discharge (like a syringe) or if the toxins are associated with the surface of the thread such that they contact the prey all along its discharged length (see Tardent and Holstein, 1982). The above results suggest that very little toxin would be injected directly into the copepod. Perhaps toxin is released into the water immediately surrounding the prey or over the surface of the prey and is taken up through the respiratory surfaces, pores such as chemoreceptors, or thin exoskeleton at the joints in sufficient quantity to narcotize or kill the prey. The extent to which the experimental prey were entangled by nematocyst threads seemed adequate to immobilize them (Fig. 4F).

Cystonect siphonophores lack nematocysts with heavily-spined or club-shaped threads that adhere to the crustacean prey captured by calycophoran and physonect siphonophores. Therefore, cystonects may be unable to entangle crustaceans and may be limited to prey types that can be penetrated by their nematocysts. The isorhizas in cystonect tentacles may be unable to penetrate the exoskeleton of crustaceans; the isorhizas are firmly anchored in the tentacle (Cormier and Hessinger, 1980), and have no structure for puncturing comparable to the stylets of stenoteles. The results of this study cannot exclude the possibility that cystonect nematocysts are stimulated to discharge only by soft-bodied prey, perhaps by a mucus coating, which is lacking in crustaceans. Nematocysts of other coelenterates discharge upon a combination of chemical and mechanical stimulation (e.g., Mariscal, 1974), and the stimulus can be quite specific in some cases (e.g., Francis, 1973; Purcell, 1977). It is also possible that the toxins of cystonect nematocysts are not effective on crustaceans. However, toxin extracted from the nematocysts of *Physalia* (the only siphonophore thus tested) killed both crabs and fish when it was injected (Lane and Dodge, 1958; Burnett and Calton, 1977).

The above data show that there are marked differences in the tentacle nematocysts of calycophoran and physonect siphonophores, and those of cystonect siphonophores, as well as marked differences in diet. The evidence suggests that the different structure of the nematocyst threads could contribute to the dietary differences; the heavily-spined threads of calycophoran and physonect nematocysts may promote entanglement of crustacean prey, while the simple threads of cystonect nematocysts may promote penetration of soft-bodied prey.

Larger prey were captured by calycophoran and physonect siphonophore species with larger nematocysts. Nematocysts of larger volumes could contain longer threads, which presumably could be more effective in entangling prey. Nematocyst discharge may be due to an increase in the internal pressure of the capsule, caused by an influx of water in response to osmotic changes in the fluid of the capsule (Lubbock and Amos, 1981; Lubbock *et al.*, 1981). The force generated for discharge could be proportional to the volume of the capsule (greater for rounded nematocysts), or to the surface-to-volume ratio of the capsule (greater for elongate nematocysts) if the reactions were surface-mediated. This idea should be testable using methods of Tardent and Holstein (1982); presently, it is only speculation.

The nematocyst batteries of calycophoran and physonect siphonophores apparently

function in two other capacities. The swimming activity of most siphonophores in these suborders serves to spread their tentacles in a 3-dimensional array (Mackie and Boag, 1963; Biggs, 1977) (Fig. 1). In *Muggiaea atlantica*, tentacle extension appears to be due to drag on the tentacles (Purcell and LaBarbera, unpub. results). Battery diameter is greater than tentacle diameter, hence the nematocyst batteries would increase drag at the ends of the tentacle branches and cause the tentacles to be drawn out. Thus, nematocyst batteries may aid in tentacle extension, enabling the spread of the tentacles to be greater and the tentacles finer (and therefore less conspicuous to prey) than possible with tentacles of uniform thickness.

Some information on morphology, behavior, and diet suggested that the nematocyst batteries of two siphonophore species may resemble small zooplankters and act to lure larger, predatory zooplankton into the siphonophore tentacles; the batteries of *Agalma okeni* resemble copepods, and some of *Athorybia rosacea* resemble fish larvae (Purcell, 1980). Further observations suggest that "lures" may occur in other siphonophore species. Two spots within the nematocyst batteries of *Nanomia cara* fluoresced when excited at 460–470 nm under an epifluorescence microscope (Purcell, unpubl. results), strongly suggesting that these spots are bioluminescent (see Morin and Reynolds, 1969). The batteries of *A. okeni*, *A. elegans*, *N. bijuga*, and *Forskalia* sp. did not fluoresce. Luminescent batteries may serve to attract prey at night or at depth, as may the luminescent lures (esca) of midwater anglerfish (Pietsch, 1974). The nematocyst batteries of *Athorybia lucida* reportedly resemble larvaceans in their houses actively pumping water (J. Trent, pers. comm.). The nematocyst batteries of *Physophora hydrostatica* began to vibrate upon the addition to the water of reduced glutathione (an inducer of feeding responses in hydrozoans, e.g., Lenhoff and Schneiderman, 1959) (Purcell, unpub. results); motion of the lures of other organisms presumably serves to attract potential prey by visual or vibrational stimuli (Pietsch and Grobecker, 1978; Purcell, 1980). There are structures on the tentacles of *Rhizophysa filiformis* that lack nematocysts, but which have a red central spot that might attract the fish larvae prey of that species (Fig. 51). These observations suggest that luring of prey by nematocyst batteries may be an important and wide-spread phenomenon, and that morphological and behavioral mechanisms underlying prey selection are unexpectedly sophisticated.

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